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Original Article

Paternal effects on access to resources in a promiscuous primate society

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The evolution of paternal care is rare in promiscuous mammals, where it is hampered by low paternity confidence. However, recent evidence indicates that juveniles whose fathers are present experience accelerated maturation in promiscuous baboon societies. The mechanisms mediating these paternal effects remain unclear. Here, we investigated whether father–offspring associations might facilitate offspring access to resources in wild desert baboons (*Papio ursinus*). We combined paternity analyses and behavioral observations of juveniles that had started feeding autonomously to show that (1) offspring associate more often with their genetic father than with any other male, and actively manage such associations, (2) offspring associate more closely with their father when another adult male is in sight, and when their mother is out of sight, (3) father–offspring associations are more frequent when juveniles are feeding (relative to other activities), and these associations enable juveniles to access richer food patches, and (4) father–offspring associations are stronger among subordinate males and their offspring. Taken together, these findings indicate that fathers may buffer the social and ecological environment faced by their offspring. In addition to mitigating risks of attacks by predators or conspecifics, paternal presence improves offspring access to food in wild baboons, highlighting a new mechanism through which fathers may impact offspring fitness in promiscuous primate societies. *Key words:* baboons, foraging success, paternal care, primates, promiscuity, reproductive strategies, sex roles. *[Behav Ecol]*

INTRODUCTION

Any behavior that a father directs toward its offspring that improves the offspring's development, growth, well-being, or survival can be considered parental care (Trivers 1972). Costly paternal care is expected to evolve only if it results in a net increase to the fathers inclusive fitness (Trivers 1972; Clutton-Brock 1991). Across taxa, paternal care is typically, albeit nonexclusively, observed when paternity confidence is high, for instance in socially monogamous birds (Møller and Cuervo 2000; Sheldon 2002) or in fish where fertilization is external (reviewed in Clutton-Brock 1991). It remains rare in mammals (e.g., approximately 10% of species: Kleiman and Malcolm 1981; Woodroffe and Vincent 1994), but occurs in up to 40% of primate genera (Kleiman and Malcolm 1981) including promiscuous species (Fernandez-Duque et al. 2009).

In promiscuous primates, the most conspicuous form of paternal care is the protection of offspring from attacks by aggressive conspecifics or predators. Although primates are at risk from a variety of predators (Cowlishaw 1994), infanticide is relatively common in primates, where males kill unrelated infants due to the long periods of female lactational amenorrhea that would otherwise limit their reproductive success (van Schaik and Janson 2000). In Hanuman langurs (*Semnopithecus entellus*), only fathers or the likely sires of an infant (i.e., males that had mated with a female during her conceptive cycle) attempted to protect it when faced with a potentially infanticidal attack (Borries et al. 1999b). Similarly, in chacma baboons (*Papio ursinus*), probable fathers carried infants when the threat of infanticide or predation was high (Busse and Hamilton 1981; Anderson 1992) and playback experiments have shown that males actively react to a threat against their probable offspring by running toward them (Palombit et al. 1997). In addition, male protection services may extend to other forms of conflicts among juveniles and other group members (Buchan et al. 2003; Lemasson et al. 2008; Moscovice et al. 2009; Nguyen et al. 2009).

However, in addition to protection services, more subtle forms of paternal care are also possible. In baboons, age at maturation occurs earlier in high-ranking females (Altmann and Alberts 2003; Johnson 2003; Wasser et al. 2004), in food-enhanced groups, or under better foraging conditions (Altmann and Alberts 2003). Because adult males can monopolize highly desirable food resources (King et al. 2008; Kaplan

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et al. 2011), father–offspring associations have the potential to facilitate resource acquisition by juveniles (Hill 1986; Kaplan et al. 2011). This "resource-acquisition" hypothesis has yet to be tested, but it could provide a proximate mechanism for the observation that the length of father–offspring coresidency in a group is linked to accelerated offspring maturation in yellow baboons (*Papio cynocephalus*), which in turn enhances lifetime reproductive success in females (and potentially males) (Charpentier et al. 2008). In addition, because such behavior may impose trivial costs to the father, it might evolve even with imperfect kin discrimination mechanisms since males would have little to lose by occasionally facilitating resource access to unrelated infants but a lot to gain by providing such access to their true offspring (see also Moscovice et al. 2009, 2010).

We investigated the benefits gained by father–offspring associations in a wild chacma baboon population. Infanticide is frequent in wild chacma baboons, where it can account for up to 75–100% offspring mortality during periods of social instability, for instance following a dominance takeover by an immigrant male (Henzi and Barrett 2003; Palombit 2003). As a counter-strategy, it has favored the evolution of heterosexual partnerships between mothers of newborns and an adult male "friend" who protects the offspring during (approximately) the first half-year of life (Palombit et al. 1997; Palombit 2000). Such friendships are common in our study population and typically involve the infant's father (Huchard et al. 2010a). Nevertheless, much less is known about the role that such former male friends may play later in an infant's life as it becomes independent from its mother, a process that is normally complete by the age of 2 years when its mother once again gives birth (Altmann 1980; Altmann and Alberts 2003). A couple of studies suggest that fathers keep on protecting juveniles from conspecific harassment when they are not vulnerable to infanticide anymore (Buchan et al. 2003; Moscovice et al. 2009). Infant mortality is high during these first 2 years of life (up to 50% in chacma baboons: Cheney et al. 2004), and is dependent not only on the risk of predation (Cheney et al. 2004) and infanticide (which can occur in infants up to 1 year of age: Palombit et al. 1997; Palombit 2000, 2003) but also on access to resources. In yellow baboons, infant survival to 2 years can be increased by up to 40% in food-enhanced groups or during favorable ecological conditions (Altmann and Alberts 2003). Thus, males may have the potential to buffer both the social and environmental challenges faced by their offspring through this vulnerable transition.

Here we examine the factors influencing the frequency and intensity of father–offspring associations during the weaning process. First, we investigate whether juveniles associate more often with their genetic father than with random males, and who (adult male or juvenile) preferentially maintains proximity. Second, we investigate whether father–offspring associations are closer when juveniles are presumably more vulnerable, when they are in the vicinity of unrelated males and when their mother is absent. Third, we test whether father–offspring associations are more frequent when juveniles feed (compared with other activities) and when they are in high-quality food patches (compared with other patches) because presence of father is predicted to facilitate offspring access to high-quality food in accordance with our "resource-acquisition" hypothesis.

METHODS

Study population

We studied wild chacma baboons living on the edge of the Namib Desert, at Tsaobis Leopard Park (22°23′S 15°45′E). Tsaobis is characterized by rocky foothills that descend to alluvial plains, bordered to the north by the ephemeral Swakop River. Baboons in this semidesert region forage in food patches, here defined as discrete shrubs or trees, found in 2 distinct habitats: closed (low-visibility) woodland and open desert (Cowlishaw 1997). The woodland occurs in groves along the Swakop and consists mainly of large trees and shrubs forming discrete food patches that can contain multiple foraging individuals. The open desert, in contrast, is characterized by herbs and scattered dwarf shrubs and trees, where food patches are rarely large enough for more than 1 individual. From these food patches, across both habitats, the baboons typically consume a range of leaves, flowers, pods, seeds, and berries. During the study period, baboons foraged almost exclusively from the woodland area.

Data were collected from October 2006 to January 2007 from 2 groups. Although this period incorporates the end of the dry season, the baboons use mostly the aquifer-dependent woodland habitat when food is scarce in the open desert, which buffers them from this scarcity. Consequently, food availability was not especially limited at this time. Study groups comprised, in October 2006, 9 adult or subadult males, 16 adult females, and 32 juveniles in the larger group (Group J) and 7 adult or subadult males, 9 females and 16 juveniles in the smaller group (Group L). All subjects were fully habituated. Both groups were captured in October 2006 to obtain biological samples, including tissue biopsies for genetic analyses (Huchard et al. 2010a, 2010b).

All 16 juveniles (8 from each group) between 6 and 24 months old at the time of the study were included (age: mean ± standard deviation [SD] = 12±0.1 months, range: 7–17 months). They were all identifiable using the ear notches made during tissue sampling while captured. Their date of birth was known from demographic monitoring of the group (12 cases), or inferred from the date of the last estrus cycle of its mother (4 cases). Infants usually start feeding on solid foods around 4–5 months of age at Tsaobis, but only reach independence later, typically between 12 and 18 months. As a result, all our subjects foraged autonomously but also still regularly suckled, except for a 1-year-old juvenile whose mother disappeared shortly before the observations started, and who was thus fully weaned. Eight mothers were in postpartum amenorrhea throughout the study and another 3 began in this state but subsequently resumed cycling (of the remainder, 1 was already pregnant whereas 4 resumed cycling shortly before the study began).

Behavioral observations

Adult dominance ranks were established using *ad libitum* and focal observations of agonistic and approach-avoid interactions (Huchard et al. 2010a). Female ranks were described as proportional rank (i.e., absolute rank/number of females in group) to control for differences in group size. Male ranks were stable throughout the study period, and coded as a binary variable (the alpha male: 1; other males: 0), because 6 adult males were included in the analyses, including 2 alpha males and 4 subordinates, respectively. No immigration events by males were recorded during the study period.

Behavioral data were collected using 1-h focal animal sampling periods (Altmann 1974) spread equally across the day (split into four 3-h time blocks) for each individual. Observations interrupted during the first 30 min were excluded from the analysis. The choice of a focal individual was randomized, and the same individual was sampled no more than once per half day. Each juvenile was followed for at least 11 h (mean ± SD = 12.9±1.1 h) for a total of 207 observation hours. Focal activity was recorded in the following categories: feeding,

resting, traveling, grooming, suckling, and playing. Changes in activity were recorded on a continuous basis. Due to the low frequency of some of these activities, grooming, suckling, and playing were pooled into a single category of "social activities."

The maintenance of spatial proximity between juvenile focal subjects and each adult male was monitored by recording close approaches and leaves to and from within 1 m of one of the dyad members (focal juvenile or adult male).

Scans were also carried out every 5 min and recorded the following information:

- Proximity of individuals in sight of the focal: identity and distance (meters) of the 2 nearest adult males, if the mother was in sight and, if so, her distance. Distance estimation was regularly checked using a range finder.
- Habitat: whether the focal juvenile was in open desert or closed woodland.

When the juvenile was in a food patch that was large enough to accommodate more than 1 individual, we recorded additionally:

- If the 2 nearest males and the juvenile's mother were also in the juvenile's patch.
- The number of adults foraging in the patch.
- Patch type, first categorized by plant species or genera (see Supplementary material, Text S1) except for smaller patches of unidentified "grasses, shrubs, and roots"; and then, if possible, by the type of food item (young leaves, flowers, berries, or pods).
- Patch quality, scored as the density of available food items on a scale of 0–10, with 0 denoting poorest quality (empty), relative to other patches of the same type. Quality scores were not available for the smaller patches classed as "grasses, shrubs, or roots." To compare the qualities of different patch types these scores were later converted into the estimated density of available food items (number of items/m^2) (see Supplementary material, Text S1 and Table S1).

Paternity analysis

All males, females, and juveniles included in this study were genotyped at 16 microsatellite loci. Full details regarding DNA sampling, extraction, microsatellite genotyping, and parentage analysis are described elsewhere (Huchard et al. 2010a, 2010b). Paternity was established for 14 of the 16 focal juveniles. In the remaining cases, defaults of assignments most likely resulted from incomplete sampling of the fathers (Huchard et al. 2010a). Among the 14 juveniles for whom paternity was known, 10 had been sired by the 2 alpha males who were still dominant at the time of the study (7 from Group L and 3 from Group J), whereas 4 (1 from Group L and 3 from Group J) had been sired by 3 subordinate males.

Statistical analyses

Our analyses occurred in 3 steps. In the first step, we investigated if juveniles displayed preferential spatial associations with their genetic father using randomization tests (see Supplementary material, Text S2), as well as who took responsibility for maintaining such associations. The responsibility for the maintenance of close proximity (within 1 m) between the 2 members of a dyad was assessed using a Wilcoxon sign-rank test for paired data; the total number of approaches (leaves) by the juvenile was compared with the total number of approaches (leaves) by the male. In the following steps, we analyzed the determinants and benefits of the preferential relationships linking each juvenile to its "behavioral" father, the male with whom he was preferentially associated. We initially focused on the adaptive value of such observed behavioral bonds—rather than relationships between juveniles and their genetic father—because the mechanisms of kin discrimination might be imperfect (Moscovice et al. 2009, 2010). Nevertheless, all the analyses presented below were also run with the genetic father, and this did not affect the results (Supplementary material, Tables S2–S4).

The second analytical step consisted in examining the factors affecting father–offspring spatial proximity. In the first analysis, we selected all scans where the father was the nearest adult male to analyze the factors influencing father–offspring distance. We used a linear mixed-effects model (LMM) with father–offspring distance ($\log_e$-transformed to comply with normality) as the response variable, and tested if presence of the mother (in sight or not), a second adult male (in sight or not), the habitat (open desert vs. closed woodland), juvenile sex, and maternal and paternal dominance rank predicted father–offspring distance. We also included 3 nested random effects: focal observation (to account for the nonindependence of scans within focal observations), nested in juvenile identity (to account for the nonindependence of repeated observations within individuals), and nested in social group identity (to account for the nonindependence of observations within groups). Note that father identity, although it is a source of nonindependence in this dataset, was not fitted as a random factor given that there are no repeated observations in a number of levels of this factor: most subordinate fathers have only sired 1 offspring. As a result, these analyses suffer from some degree of pseudoreplication which cannot be accounted for statistically, and is partly inherent to the biology of our system—where reproduction is monopolized by a limited number of males. For this and further analyses, we removed focal observations with less than 3 scans (to ensure that parameter estimates of the "focal observation" random effect relied on a sufficient number of scans). We then went on to analyze all scans where the juvenile was located in a food patch and where the father's position was recorded (in or out the food patch) to identify those factors that might influence the presence of the father within the juvenile patch (our binary response variable). We performed a generalized linear mixed-effect model (GLMM) with binomial error distribution and a logit link function to test what factors predicted father–offspring association. We tested a number of fixed effects: the presence of the mother and a second adult male within the patch, juvenile activity, the number of adults present within the patch, juvenile sex, and the maternal and paternal dominance rank. Including the number of adults present within the patch at the time of the scan aimed at controlling for patch size and attractiveness, thus ensuring that any factors affecting the probability of father–offspring association were not a spurious consequence of an increased number of individuals in large and attractive patches. We considered the same random effects as above.

In the last analytical step, we examined the factors influencing juvenile access to high-quality food patches. We restricted this analysis to those patches where the juvenile actively foraged, because they often rest or play when adults are feeding and the quality of the patch might not be important on such occasions. In the first model, we tested whether father or mother presence within a patch facilitated juvenile access to high-quality patches (a binary response variable: "high" or "low" quality) using a GLMM with a binomial error distribution and a logit link function. We restricted our dataset to scans collected when the baboons were foraging on the honey mesquite *Prosopis glandulosa*—a primary food resource during the study season—because our quality scoring system only ranked patch quality relative to other patches of the same type. We divided the dataset between patches of high quality

(scored ≥6) and of low quality (scored ≤3), and excluded other patches. In a second model, we analyzed the influence of the same factors on the density (number of items/m^2) of food items in the patch, including all the patches for which a density score was available (not just *Prosopis*), using a LMM with the same random effects as those listed above. This response variable was $\log_e$-transformed to comply with normality.

Throughout, the significance of fixed effects was tested using the full model (i.e., with all predictors present) (Whittingham et al. 2006; Mundry and Nunn 2009). All GLMMs and LMMs were run with Proc Glimmix on SAS V9.2.

RESULTS

Do offspring preferentially associate with their father?

Among the 14 focal juveniles for whom the genetic father was known, we collected a total of 1465 (out of 2352) proximity scans in which the identity of the nearest adult male was recorded (mean ± SD: 104.6±15.1 scans per juvenile, range: 81–129). The father was present in 40% of all scans and was the nearest adult male in a total of 65% of these scans (mean ± SD = 64±18% scans per juvenile, range: 31–95%). The number of juveniles (12 out of 14) associating with their genetic father more than with any other male was higher than expected by chance (randomization test, mean ± SD = 3.19±1.57, $P < 0.001$). The 2 remaining offspring nevertheless associated preferentially with 1 adult male (45% of scans in both cases, compared to a range of 0–30% for any other male). In one case the preferred male was an older maternal sibling, and in both cases the father was the second most frequent nearest adult male.

Father–offspring proximity appeared to be maintained by the juveniles, who approached their father more often than the reverse (Wilcoxon sign-rank test for paired data, $N = 16$, $V = 103.5$, $P = 0.001$) and left their father more often than the reverse (Wilcoxon sign-rank test for paired data, $N = 16$, $V = 86.5$, $P = 0.005$).

Which factors modulate father–offspring distance?

Offspring were closer to their father when a second adult male was in sight (Table 1, Figure 1a) and when the mother was out of sight. Although neither juvenile sex nor habitat affected father–offspring distance, juveniles born to high-ranking mothers and from subordinate fathers (Table 1, Figure 1b) maintained closer proximity to their father.

Do father–offspring associations increase offspring access to resources?

We then examined the factors affecting the probability of father–offspring association in food patches (Table 2). A juvenile was more likely to be in the same patch as its father when a second adult male was also present in the patch (Figure 1c). Our model controlled for the number of other adults present, which means that the effect of a second male should not have arisen from a "crowding effect" in larger or more attractive patches. In addition, feeding was the activity that most increased the probability of father–offspring association in food patches, suggesting that offspring join their father when foraging (Figure 2a) but such associations were independent of the mother's presence. Finally, the probability of father–offspring associations in feeding patches was independent of juvenile sex and maternal rank, but was higher when the father was subordinate (Figure 1d).

To further examine whether a father's presence facilitates his offspring's access to resources, we restricted the dataset to those scans for which the juvenile was feeding. In our first model, restricted to *Prosopis* food trees, we found that a juvenile's presence in high-quality patches was associated with the father's presence (Table 3, Figure 2b). The same results were obtained in our second model, across all food patches (Table 3, Figure 2c). In contrast, the mother's presence had no effect in either case.

DISCUSSION

Our results show that young baboons associated preferentially with their father over other males, and were closer to their father when another adult male was in the vicinity or when their mother was absent. These results lend support to the idea that males offer "protection services" to infants, which may reduce the risk of predation and conspecific aggression. We also found strong support for our "resource-acquisition" hypothesis; paternal presence increased offspring access to higher quality resources independently of maternal presence. Our study thus identifies a novel mechanism through which paternal presence might increase offspring fitness.

Our findings imply that father and offspring are often able to recognize their genetic relationship, supporting previous findings in promiscuous primate societies (Borries et al. 1999a; Buchan et al. 2003; Charpentier et al. 2007; Lehmann et al. 2007). Although this study does not

Table 1

Determinants of father–offspring distance involving 16 juveniles and their behavioral father ($n = 5$ males)

Response variable	Fixed factors	β ± SD	*F*-value	Degrees of freedom (df)	*P*
Father–offspring distance (m) ($n = 1016$ scans)	Nearest second adult male in sight (y/n)[a]	0.21±0.07	8.01	1, 1014	$<10^{-2}$
	Mother in sight (y/n)[a]	−0.16±0.07	4.56	1, 1014	0.03
	Habitat (open vs. closed)[b]	0.08±0.10	0.65	1, 1014	0.42
	Juvenile sex[c]	0.08±0.15	0.26	1, 1014	0.61
	Maternal rank	−0.55±0.24	5.44	1, 1014	0.02
	Paternal rank[d]	0.65±0.15	20.1	1, 1014	$<10^{-4}$

The response variable was $\log_e$-transformed. The parameters and tests were computed using GLMMs controlling for the nonindependence of scans within focal observations, the repeated appearance of focal individuals, and the potential nonindependence of data collected from the same social group. β: estimate of the fixed factor and SD: standard deviation. These results were unaffected when this model was run for 14 father–offspring associations involving only juveniles with known paternity and their genetic fathers (see Supplementary material, Table S2).

[a]Reference category: yes.

[b]Reference category: closed riverbed.

[c]Reference category: male.

[d]Reference category: nonalpha.

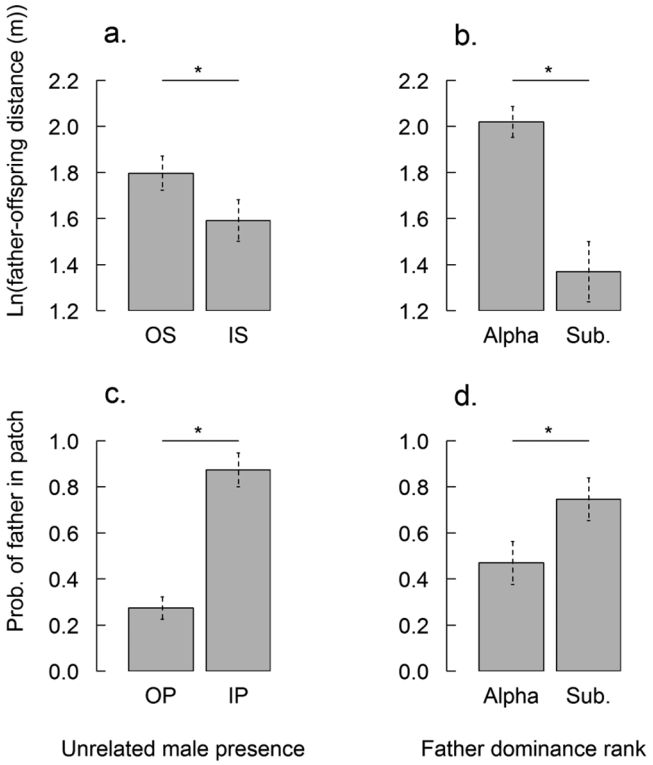

Figure 1
Determinants of father–offspring distance and associations in food patches. (a) Influence of the presence of a nonfather male in sight on $\log_e$(father–offspring distance); IS, in sight; OS, out of sight. (b) Influence of the father's dominance rank on $\log_e$(father–offspring distance); Sub.: subordinate. (c) Influence of the presence of a nonfather male on the probability of father–offspring association in food patches; IP, in patch; OP, out of patch. (d) Influence of the father's dominance rank on the probability of father–offspring association in food patches. Bars represent predicted means and SD computed from the model estimates (and adjusted for other covariates). $*P < 0.05$.

address the mechanisms underlying kin discrimination, it suggests that father–offspring bonds are formed early in life. In this cohort, most male–juvenile dyads extended the friendship linking the juvenile's parents after its birth (Huchard et al. 2010a): in 13 of 15 cases (where the juvenile's mother had been observed during the first 3 months after birth), the juvenile's behavioral father was also the male who shared most proximity and grooming with the mother soon after birth. Because mothers are primarily responsible for the formation and maintenance of these heterosexual relationships (Palombit et al. 1997; Huchard et al. 2010a), they may play an important role in promoting paternal tolerance to the proximity of familiar juveniles later in life. Indeed, it is possible that this might constitute the mechanism by which father–offspring kin discrimination occurs.

Father–offspring proximity was actively maintained by juveniles, suggesting that fathers do not contribute to maintaining such spatial affiliations. However, in most mammals, offspring typically follow their parents, so this pattern should not appear surprising in a society where movements are primarily led by adult males (King et al. 2008, 2011). Moreover, father passivity in proximity maintenance does not necessarily imply passivity in maintaining social relationships. Previous reports of paternal interventions in support of offspring during conflict with conspecifics clearly indicate that fathers readily take an active role when their offspring is threatened (Palombit et al. 1997; Borries et al. 1999a; Buchan et al. 2003; Huchard et al. 2010a). In particular, playback experiments have shown that behavioral fathers run toward juveniles when they hear their screams (Moscovice et al. 2009).

Father–offspring bonds apparently serve multiple functions. Supporting our predictions, juveniles were closer to their father when their mother was out of sight, and when another adult male was in sight. These findings suggest that juveniles seek paternal protection when they are vulnerable, especially to aggression from conspecific adult males, in line with previous work on baboons and other primates (Palombit et al. 1997; Borries et al. 1999a; Buchan et al. 2003; Moscovice et al. 2009; Huchard et al. 2010a). Nevertheless, several observations suggest that infanticide risk is low for this juvenile cohort: first, juveniles had passed the critical window of vulnerability to infanticide (0–6 months), and half of their mothers had already resumed cycling. Second, no male had recently immigrated into either of the study groups, and more than half of the juveniles had been sired by the current dominant male. As a result, infanticide risk might not

Table 2

Determinants of father–offspring association in food patches involving 16 juveniles and their behavioral father (n = 5 males)

Response variable	Fixed factors	β ± SD	*F*-value	df	*P*
Association with father in food patches (y/n) (n = 949 scans)	Nearest second adult male in patch (y/n)[a]	−2.89 ± 0.64	20.23	1, 948	$<10^{-4}$
	Mother in patch (y/n)[a]	0.22 ± 0.37	0.33	1, 948	0.56
	Juvenile activity[b]				
	Feeding	1.04 ± 0.43	6.68	1, 948	$<10^{-3}$
	Resting	−0.32 ± 0.50			
	Social activity	−0.09 ± 0.63			
	Number of adults in patch	1.05 ± 0.10	120.94	1, 948	$<10^{-4}$
	Juvenile sex[c]	0.32 ± 0.46	0.49	1, 948	0.48
	Maternal rank	0.11 ± 0.71	0.02	1, 948	0.87
	Paternal rank[d]	−1.19 ± 0.43	7.72	1, 948	$<10^{-1}$

The parameters and tests were computed using GLMMs controlling for the nonindependence of scans within focal observations, the repeated appearance of focal individuals, and the potential nonindependence of data collected from the same social group. β: estimate of the fixed factor and SD: standard deviation. These results were unaffected when the model was rerun for 14 father–offspring associations involving only juveniles with known paternity and their genetic fathers (see Supplementary material, Table S3).
[a]Reference category: yes.
[b]Reference category: travel.
[c]Reference category: male.
[d]Reference category: nonalpha.

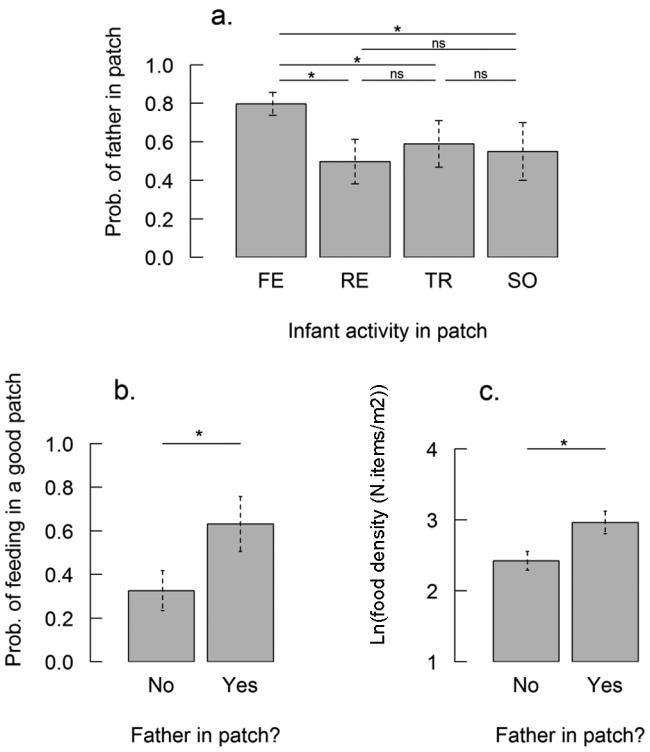

Figure 2
Paternal effects on offspring access to food. (a) Influence of the juvenile's activity on the probability of father–offspring association in food patches. Focal activities are labeled FE (feed), RE (rest), TR (travel), and SO (social). (b) Influence of paternal presence on juvenile access to *Prosopis glandulosa* patches. (c) Influence of paternal presence on juvenile access to patches containing a high density of food items. Bars represent predicted means and SD computed from the model estimates (and adjusted for other covariates). $*P < 0.05$. ns, nonsignificant.

represent the primary determinant of father–offspring associations observed here, although juveniles may still seek protection against other forms of harassment by, or conflict with conspecifics (Buchan et al. 2003; Moscovice et al. 2009).

Our results further revealed that juveniles were more often found with their father when feeding. This pattern occurred above and beyond the potential confounding effects of crowding in large patches and mother–father bonds (we controlled for both the number of adults and maternal presence, respectively). Foraging juveniles were also more likely to be found in high-quality food patches when in the company of their father (both within and across food types). These findings suggest that paternal tolerance improves offspring foraging opportunities by facilitating access to the best patches. Maintaining close proximity to its father might allow a juvenile to enter and feed in high-quality patches from which it would otherwise be excluded, given that such patches are typically monopolized by high-ranking males (King et al. 2008). As such, the fact that juveniles avoid the proximity of males other than their father can be understood in light of the "resource-acquisition" hypothesis, if juveniles learn who does and who does not allow effective feeding in close proximity. It might also help offspring to reach autonomy in selecting resource types through observational learning (Pereira 1988; Thornton and McAuliffe 2006; Rapaport and Brown 2008). Consistent with our observations, previous research has also shown that high-ranking males monopolizing access to artificial feeding arenas tolerate the presence of some juveniles, albeit whose paternal status is unknown (rhesus macaques: Hill 1986; chacma baboons: Kaplan et al. 2011).

The benefits of enhanced food acquisition on juvenile survival, growth rates, and age at sexual maturity have been reported in several primates (Mori 1979; Lyles and Dobson 1988), including baboons (Altmann and Alberts 2003; Johnson 2003; Wasser et al. 2004). In this context, our findings highlight a potential mechanism underlying the positive effect of the length of father–offspring troop coresidency on offspring age at maturation reported in yellow baboons (Charpentier et al. 2008). More generally, the facilitation of resource acquisition by fathers might represent an important and under-appreciated mechanism through which primate males can enhance offspring fitness, without paying substantial costs. Finally, the closer association observed among males and juveniles born from high-ranking mothers suggests that the multiple benefits of high maternal rank (Altmann and Alberts 2003; Johnson 2003; Wasser et al. 2004) extend to paternal effects, indicating a further mechanism through which female dominance rank might enhance offspring survival and fitness in baboon societies.

Tolerating the presence of juveniles might benefit adult males in 2 ways: it might either enhance the survival of their offspring or promote their future chances to mate with the infant's mother (if paternal care functions as a courtship strategy: Strum 1984; Smuts 1985). Although these hypotheses are not mutually exclusive, our findings provide more support for the offspring survival hypothesis based on 3 main points: (1) male–juvenile associations occur preferentially among related dyads, (2) the benefits of these associations to offspring fitness are clearly identified, and (3) these associations are

Table 3

Determinants of juvenile access to high-quality food patches involving 16 juveniles and their behavioral father ($n = 5$ males)

Response variable	Fixed factors	β ± SD	*F*-value	df	*P*
Quality of *Prosopis* patch ($n = 319$ scans)	Father in patch (y/n)[a]	−0.27 ± 0.54	5.53	1, 317	0.02
	Mother in patch (y/n)[a]	0.16 ± 0.64	0.06	1, 317	0.80
Density of food items in patch ($n = 628$ scans)	Father in patch (y/n)[a]	−0.54 ± 0.15	13.84	1, 626	$<10^{-3}$
	Mother in patch (y/n)[a]	−0.14 ± 0.15	0.89	1, 626	0.35

For the first response variable, patch quality was scored on a quantitative scale (0–10, with 0 for the worst patches); for the second response variable, patch quality scores were converted to density of food items. The parameters and tests were computed using GLMMs controlling for the nonindependence of scans within focal observations, the repeated appearance of focal individuals, and the potential nonindependence of data collected from the same social group. β: estimate of the fixed factor and SD: standard deviation. These results were unaffected when the model was rerun for 14 father–offspring associations involving only juveniles with known paternity and their genetic fathers (Supplementary material, Table S4).
[a]Reference category: yes.

largely independent of the mother's presence. In this context, the higher intensity and frequency of father–offspring bonds among subordinate males might suggest that such males try to compensate for their limited mating prospects by increasing their care for their infants. However, because juveniles actively maintain spatial proximity to their fathers, it is likely that this pattern also, or primarily, reflects a juvenile strategy. Juveniles fathered by subordinate males might indeed be at greater risk of infanticide by dominant males (Huchard et al. 2010a). Alternatively, juveniles may compete for proximity to fathers, and the lower competition around subordinate males (who have fewer offspring) may explain their closer father–offspring associations.

The occurrence of male care in mating systems with low paternity certainty can be understood in 2 ways: either male care is costly and kin discrimination mechanisms are effective or males only engage in low-cost paternal care toward juveniles for which the probability of paternity is sufficiently high to balance the costs incurred. Earlier work (Borries et al. 1999a, 1999b; Buchan et al. 2003) has suggested that kin discrimination is highly effective. Yet, recent findings indicate that such mechanisms are probabilistic (Moscovice et al. 2009, 2010), such that males may be able to differentially invest in juveniles according to their level of paternity certainty. Our discovery of a mechanism through which fathers might facilitate offspring access to food without facing high costs is consistent with the latter view, and opens up the possibility that paternal strategies may increase offspring fitness without compromising their future reproductive success in promiscuous societies.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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